

**South American rocky habitat *Leptodactylus*
(Amphibia: Anura: Leptodactylidae)
with description of two new species**

W. Ronald Heyer

Department of Vertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Abstract.—There are four groups of populations of *Leptodactylus* associated with rocky habitats in northern South America. The available data are most consistent with recognizing three species for these four units: *L. rugosus* and two new species, *L. lithonaetes* and *L. myersi*. A single specimen from Paraguay, although distinctive, is considered to be conspecific with *L. syphax*, previously known from disjunct localities in eastern Brazil. Data are inadequate at present to determine whether the South American species of *Leptodactylus* associated with rocky habitats are a monophyletic group.

Charles W. Myers brought my attention to a distinctive new species of the frog genus *Leptodactylus* that he had collected from granitic outcrops in the State of Roraima, Brazil. As study of the material progressed, comparisons were made between the new species from northern Brazil with *Leptodactylus rugosus*, a species from granitic and sandstone habitats of the Guiana shield region. It became apparent that there was considerably more variation among populations of the Guiana shield frogs than recognized previously (Heyer 1979). From the other end of South America, a single specimen of *Leptodactylus* was collected several years ago from rocky outcrops in Paraguay; this specimen's affinities are problematic. The purpose of this paper is to re-evaluate the species status of the *Leptodactylus* associated with granitic and sandstone habitats in South America.

Methods and Materials

As aspects of variation in *Leptodactylus syphax* have recently been addressed (Cardoso & Heyer 1995), members of that species are not treated in detail here. As many specimens as possible were borrowed of all

other granitic and sandstone habitat *Leptodactylus*. Data were taken on patterns of the dorsum, upper lip, posterior thigh, and upper shank using the standards described in Heyer (1979). In addition, belly and ventral thigh surface patterns were recorded. Information was noted on dorsal folds, texture of the dorsum, upper shank, outer tarsus, and foot, as well as male secondary sexual characteristics. The snout–vent length (SVL) was recorded for all specimens. For all adults and specimens near adult size, the following measurements were also recorded (following Heyer et al. 1990): head length (HL), head width (HW), eye–mid-nostril distance (E–N), tympanum diameter (TD), thigh, shank, and foot. Statistics were analyzed with SYSTAT for Windows, version 5 (1992). Museum abbreviations are those recommended by Leviton et al. (1985) with the addition of IND-AN = INDERENA, Ministerio de Agricultura, Bogotá, Colombia.

Variation in Northern South American Rocky Habitat *Leptodactylus*

As data were being collected on specimens from northern South America, it be-



Fig. 1. Localities for Group 1-4 specimens from northern South America. Group I = dots (*L. lithonaetes*), Group II = squares (*L. rugosus*), Group III = triangles (*L. myersi*), Group IV = circles (*L. myersi*).

came apparent that there were four groups involved based on character states and geographic distributions. Each group is discussed in some detail and then decisions are drawn with respect to species limits. There are few tadpole samples; those that are available do not all contain Gosner (1960) stage 25-32 specimens. Tadpole characteristics described in this section are based on Gosner stage 33-42 specimens. Because recordings of advertisement calls exist for only Group 2 individuals, those data are not discussed.

Group 1.—Specimens in this group are from Colombia and Venezuela near the Colombian border (Fig. 1). Seventeen adult females, 31 adult males, 176 total specimens.

Dorsal patterns characteristically have a series of 3-4 (rarely 2) pairs of spots ranging from small to large in size and ranging from discrete to patterns of fusion with other spots both across, as well as, lengthwise along the dorsum (Heyer 1979, fig. 1, patterns H through K). About 10% of the individuals have a uniform dorsum.

Upper lip patterns show a continuum among the following states. Thirteen percent of the specimens have little pattern on

the upper lip (Heyer 1979, fig. 2, patterns C, E); 32% have some expression of alternating light and dark vertical bars (Heyer 1979, fig. 2, pattern J); 29% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); and 26% have some sort of irregularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, pattern M).

The posterior thigh surface pattern also shows a complete continuum among the following conditions. The posterior thigh surfaces are indistinctly mottled in 39% of the individuals (Heyer 1979, fig. 3, pattern P); distinctly mottled with small light irregular marks in 17% of the individuals (Heyer 1979, fig. 3, patterns B, C, D); distinctly mottled with large light irregular spots and marks in 38% of the individuals (Heyer 1979, fig. 3, pattern A); 5% of the individuals have distinctly mottled thigh surfaces with some expression of light vertical marks or bars on the upper portions of the thigh surfaces (Heyer 1979, fig. 3, pattern D); one individual has a large light area on the lower thigh surface containing a few distinct dark spots; one individual has a large light area on the upper thigh surface.

One juvenile has a distinct lengthwise light band in the middle of the ventral thigh surface, 8% of the juveniles have a noticeable light band, whereas no adults have any indication of such a band; 76% of juveniles and 44% of adults have very light ventral thigh surfaces with few or no melanophores (Fig. 2); 9% of juveniles and 33% of adults have almost uniformly dark ventral thigh surfaces; 3% of juveniles and 12% of adults have lightly to moderately mottled ventral thigh surface patterns; 3% of juveniles and 10% of adults have the upper-lateral sector boldly mottled and the rest of the ventral thigh surface uniformly light.

Sixteen percent of the juveniles and 45% of the adults have relatively uniform gray/brown bellies, although in some, the posterior belly is lighter than the anterior; 50% of the juveniles and 2% of the adults have uniformly light bellies with very few melanophores (Fig. 2); 9% of the juveniles and 22% of the adults have dark bellies with moderate to low contrast light spots and/or vermiculations; 1% of the juveniles and 16% of the adults have a mottled pattern of smaller irregular lighter areas on a darker ground; and 24% of the juveniles and 14% of the adults have a bold mottled pattern of large light spots/flecks on a darker ground color.

Dr. Charles W. Myers (pers. comm.) provided life color information based on specimens AMNH 100656–100667 from the southwest sector of Cerro Yapacana, Amazonas, Venezuela: “Small white markings on lip. Rear of thigh usually suffused with orange (dotted pale tan on black in one specimen). Ventral surfaces grayish white. Juvenile (small specimen, 14875) [= AMNH 100666, 20.7 mm SVL] has pure white venter and bright orange under thighs, and a strong suffusion of orange on rear of thigh. Iris overall pale bronze, or pale bronze above and pale gray below—with overall dense black venation.” Dr. John D. Lynch (pers. comm.) provided life color information based on specimens from Cueva Arévalo, Vichada, Colombia, es-

pecially ICNMNH 13972–13974: “Dorsum brown with slightly darker brown and black spots on upper flanks. Patches on head and center of back rust. Pale brown (almost cream) interorbital bar and some marks on back. Face cream with black canthal stripe. Tympanum reddish-brown. Limb bands black. Yellow warts on flanks (glands). Venter and throat cream with brown spots and reticulation. Undersides of thighs pink. Posterior surfaces of thighs marbled black with faint rose spots. Iris bright copper above, gray below, flecked with black and bearing black horizontal streak. Other individuals may have posterior thighs black with small yellow spots above, becoming more rose below. Dorsum varies from tan to nearly black. In males the lateral $\frac{1}{3}$ of the gula is black (center white). Face generally pale (some dark individuals do not have the pale labial patch). Venter scarcely to heavily spotted with brown. Some dorsal patches have olive cast. Variation based on series of 15 individuals. . . .”

The degree of juvenile and adult pattern differences from individuals from the same localities, although noticeable in preserved specimens, is not striking. The most noticeable features are that the bellies and ventral thigh surfaces are lighter than in the adults, but these differences are more of degree than fundamentally different.

The commonest conditions for dorsolateral fold development are either no indication of dorsolateral folds or one short pair of ridges or elongate warts in the shoulder region. Some specimens have series of warts or ridges in the dorsolateral fold field, some extending the entire length of the dorsum from behind the eye, others extending only to the sacrum.

Most individuals have a shagreen together with black and/or white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Most juveniles (80%) either have a moderate to pronounced shagreen and/or small bumpy glands without any black and/or



Fig. 2. Characteristic ventral patterns of juveniles. Upper left, Group I, ICNMNH 13980; upper right, Group II, USNM 291249; lower left, Group III, AMNH 128023; lower right, Group IV, RMNH 23921.

white tubercles; 31% of adults lack tubercles.

The upper shank surface may have a shagreen or not. Most specimens (93%) have few to many black and/or white tubercles; few specimens (7%) have very few or no tubercles.

The texture of the outer tarsus may be shagreened or not. Most specimens (81%) have few to many black and/or white tubercles; some specimens (19%) have very few or no tubercles.

Texture of the foot is usually smooth, lacking shagreen or tubercles (86%); some

individuals (12%) have no more than a few black and/or white tubercles; very few individuals (2%) have a weakly developed shagreen.

Adult males have one black thumb spine on each hand and a pair of chest spines. There is also a band of black tubercles across the chest in larger males. Males have a patch of black chin tubercles on the anterior portion of the throat. The vocal sacs are laterally expanded and darkly pigmented.

Adult females range between 54.8 and 78.4 mm SVL, adult males 45.3 and 71.4 mm SVL. A principal components analysis was run on the measurement data for adult specimens. No obvious outliers are evident on the resultant plot of individuals using the first two factors.

Two series of tadpoles are available, one well-preserved series of specimens from Cerro Patavá, Colombia, and two alcohol preserved dehydrated specimens from Canaripo, Venezuela. It is difficult to determine to what degree the differences observed between larvae from these two localities are due to preservation artifact. Tadpoles from both localities demonstrate the semiterrestrial ecomorph as described by Altig & Johnson (1989). The body length is 28–31% of the total length in the Cerro Patavá tadpoles, 31–32% in the Canaripo tadpoles. The anterior oral gap is 80–88% of the oral disk width in the Cerro Patavá specimens, 64–77% in the Canaripo specimens. The upper beak is highly arched; its depth is 27–37% of the upper beak width in the Cerro Patavá sample, 36% in the Canaripo sample. The body is flattened, with body depth 67–74% of body width in the Cerro Patavá larvae, 46–56% in the Canaripo larvae. Larvae have series of glandular ridges on the body above the abdominal cavity.

Habitat notes are available from AMNH 100656–100667 collected at Cerro Yapacana, Amazonas, Venezuela, 18–19 February 1978 (C. W. Myers, pers. comm.): “Mountain stream by night, sitting on the rock stream bed at or near edge of water.

... They are timid and quick to take cover in crevices and under large boulders if one's light is not kept on them while approaching; they seem to avoid diving into the water.”

Group 2.—This group includes specimens from Guyana and southeastern Venezuela (Fig. 1). Seventeen adult females, 35 adult males, 126 total specimens.

Most specimens have a dorsal pattern of a series of 3–4 (rarely 2) pairs of large to small spots ranging from discretely defined to patterns of fusion with other spots both across the dorsum as well as lengthwise along the dorsum (Heyer 1979, fig. 1, patterns H through K). Twenty-seven percent of the individuals have uniform or almost uniform dorsal patterns.

Upper lip patterns represent a continuum among the following states. Eleven percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 8% have some expression of alternating light and dark vertical bars (Heyer 1979, fig. 2, pattern J); 43% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); 26% have some sort of irregularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, pattern M); 7% have an irregularly defined light area in the loreal region, separated from light oblique bars behind the eye by irregular dark bars (Heyer 1979, fig. 2, pattern K); and 3% have extensive dark mottling on the upper lip, heaviest near the mouth.

Posterior thigh surface patterns are quite variable, with a continuum including the following states. The posterior thigh surfaces are indistinctly mottled in 8% of the individuals (Heyer 1979, fig. 3, pattern P); distinctly mottled with small light irregular marks in 4% of the individuals (Heyer 1979, fig. 3, patterns C, D); distinctly mottled with large light irregular spots and marks in 40% of the individuals (Heyer 1979, fig. 3, pattern A); the upper thigh surfaces have some sort of light vertical marks or bars in 15% of the individuals (Heyer 1979, fig. 3, patterns E, F); the lower thigh

surface has one or more extensive light area, sometimes with a few small dark spots in 22% of the specimens; and the upper thigh surface has a large light area in 10% of the individuals.

The ventral thigh surfaces are very light with few or no melanophores in 72% of the juveniles and 31% of the adults (Fig. 2); the ventral thigh surfaces are almost uniformly dark in 13% of the adults (no juveniles); the ventral thigh surfaces are lightly to moderately mottled in 5% of the juveniles and 37% of the adults; the ventral thigh surfaces have the upper-lateral sector boldly mottled with the rest of the thigh surface uniformly light in 23% of the juveniles and 18% of the adults.

Two percent of the juveniles and 21% of the adults have relatively uniform gray/brown bellies; 44% of the juveniles and 13% of the adults have almost uniformly light bellies with very few melanophores (Fig. 2); 3% of the juveniles and 8% of the adults have dark bellies with moderate to low contrast light spots and/or vermiculations; 17% of the juveniles and 45% of the adults have a mottled pattern of smaller irregular lighter areas on a darker ground; and 33% of the juveniles and 13% of the adults have a boldly mottled pattern of large light spots/flecks on a darker ground.

Donnelly & Myers (1991:22) provided color descriptions for specimens from Cerro Guaiquinima, Bolívar, Venezuela: "In life, some juveniles had white-edged dorsal blotches whereas others were uniformly blackish. The throat was heavily marked with gray mottling on white and there was less gray on the venter. The body glands of the groin and the ventral and posterior thigh surfaces had variable suffusion of orange that was bright in some individuals. The iris was bronze above, white on the medial ventral section, and brown between, with dense black venation overall." Dr. Robert P. Reynolds (pers. comm.) provided copies of his color notes for specimens from Kaieteur Falls, Guyana. A series of adults and small juveniles (USNM 291245–291250) had the

following: "Brown dorsally with warty rugose skin. . . . Venter cream with darker mottling. Rose-orange groin and undersurfaces of thighs. Bronze-gold iris." A female (USNM 291251) was: "Dorsally greenish with dark speckling throughout. Rims of eyelids yellowish with yellow band between eyelids. Three–4 light spots on lower eyelid. Yellowish with mottled brown between upper lip and eyelid. Tympanum rust brown. Iris bronze. Venter brownish with white throughout. Rear of thigh gold and brown mottled." A series of adults of both sexes (USNM 291252–291256) were: "Dorsally greenish brown with yellow mottling. Three distinct yellow lines from eye to lip. Yellow line between eyes on top of head and a line from rear of each eye back to rear of head. Rust wash over neck and shoulder area. Mottled light and dark venter. Undersides of legs rose tint with dark spots." A single male (USNM 342151) had: "Dorsum reddish brown, limbs with reticulate dark markings, light line between orbits, bronze eye, dark canthal stripe; chin, throat, chest and belly with dark grey spotting, underside of thighs and calfs salmon red."

The degree of juvenile and adult pattern differences from individuals from the same localities are striking with respect to ventral patterns, especially when small juveniles are compared with adults. The throats and bellies of juveniles are bright white in recently preserved specimens (Kaieteur National Park, Guyana), whereas the throats and bellies of adults are densely mottled dark gray; the ventral thigh surfaces of the juveniles lack melanophores and stand in contrast to the dark pigmented ventral thigh surfaces of adults. No differences in dorsal pattern between juveniles and adults are evident.

The commonest conditions for dorsolateral fold development are either no indication of dorsolateral folds or one short pair of ridges or elongate warts in the shoulder region. Three individuals were recorded as having two pair of short ridges and three

individuals were recorded as having a series of short ridges in the dorsolateral fold field.

Most individuals have a shagreen and black and/or white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Twenty-two percent (20 individuals) of the juveniles have a pronounced dorsal texture of a strongly developed shagreen with glandular warts; only 5% (2 individuals) of the adults have the same texture.

The upper shank surface may have a shagreen or not. Almost all specimens (122 of 124 recorded) have few to many black and/or white tubercles; only 2 individuals have very few or no tubercles.

The texture of the outer tarsus may be shagreened or not. Almost all specimens (98%) have few to many black and/or white tubercles; only 2 individuals (2%) have very few or no tubercles.

The texture of the foot is smooth, lacking shagreen or tubercles in 50% of the individuals; 49% of the specimens have no more than a few black and/or white tubercles; very few individuals (2%) have a weakly developed shagreen.

Adult males have one or two black thumb spines on each hand and a pair of chest spines. There is no distinctive band of black tubercles across the chest in larger males. Males lack a patch of black chin tubercles on the anterior portion of the throat. The vocal sacs are laterally expanded and darkly pigmented.

Adult females range between 53.6 and 73.5 mm SVL, adult males 50.9 and 71.6 mm SVL. A principal components analysis was run on the measurement data for adult specimens. There is a general cluster of points on the plot of individuals using the first two factors, but three individuals lie somewhat outside the general cluster. KU 166499 is an individual from a locality in which all other specimens lie in the general cluster of points. RMNH 23906 and USNM 258130 are the only adult individuals from each of two different localities. Re-examination of these specimens does not indicate

that any change should be made in their assignment to the geographically based four clusters.

Data were taken from a single tadpole from Cerro Auyantepui, Venezuela, a single tadpole from La Escalera, Venezuela (both alcoholic) and seven larvae from Kartabo, Guyana (formalin). These tadpoles demonstrate the semiterrestrial ecomorph as defined by Altig & Johnson (1989). The body length is 28–29% of the total length. The anterior oral gap is 75–81% of the oral disk width. The upper beak is highly arched; the upper beak depth is 33–40% of the upper beak width. The body is flattened; the depth is 64–70% the body width. Larvae have series of glandular ridges on the body above the abdominal cavity.

Habitat information specific for members of Group 2 has been published by Donnelly & Myers (1991:22) for specimens from Cerro Guaiquinima, Bolívar, Venezuela: "Adults were taken at night in the rocky stream bed at Camp 2 and in the north stream at Camp 1. At Camp 2, several adults were collected by night in water in the middle of small waterfalls. Juveniles were active both day and night. During the day, juveniles were commonly seen in exposed situations, sitting on rocks around small pools and jumping into the pools when disturbed." Robert P. Reynolds (pers. comm.) collected a series of specimens (including USNM 291245–291256) at night at Kaieteur National Park, Guyana, 29–30 March 1989, on a trail from the airstrip to the guest house above Kaieteur Falls. Some individuals were calling and others were not. On the afternoon of 7 April 1994, Reynolds collected USNM 342151–342160 on bedrock puddles, near the airstrip at Kaieteur Falls.

Group 3.—Specimens from this group are from northern Brazil (Fig. 1). Three adult females, 13 adult males, 47 total specimens.

The dorsal patterns characteristically have two large dark spots on the dorsum (Heyer 1979, fig. 1, pattern K). The spots may have fuzzy borders, or be well defined

with a black outline border, or be well defined by a contrasting light border. The spots may be fused with each other and the interocular spot. Nine percent of the individuals have a dark dorsum with a few small, discrete, irregular, lighter spots. One individual has paired series of dark dorsal spots (Heyer 1979, fig. 1, pattern H). No individual has a completely uniform dorsum.

Upper lip patterns demonstrate a continuum among the following states. Nine percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 49% have some expression of dark vertical bars (Heyer 1979, fig. 2, patterns A, J); 16% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); 20% have some sort of irregularly to regularly defined light area in the loreal region to under the eye (Heyer 1979, fig. 2, patterns L, M); and 7% have a mottled upper lip with small dark spotting.

The posterior thigh surface patterns grade among the following states. A single individual has an indistinctly mottled posterior thigh surface (Heyer 1979, fig. 3, pattern A); one specimen has an almost uniformly dark thigh surface; 70% have large light spots on the upper portion of the posterior thigh surfaces with or without smaller light spots on the lower portion of the posterior thigh surfaces; 15% have narrow vertical light stripes on the upper portion of the posterior thigh surface; and 11% have few to several distinct small light spots on the posterior thigh surface (Heyer 1979, fig. 3, patterns N, O).

Most juveniles (79%) have at least a noticeable lengthwise light band in the middle of the ventral thigh surfaces (very distinct in 38% (Fig. 2)), whereas only one adult has a faint indication of this band; one juvenile and most adults (69%) have almost uniformly dark gray or brown ventral thigh surfaces; 17% of the juveniles and 25% of the adults have lightly to moderately mottled ventral thigh surfaces.

No juveniles, but 29% of the adults, have relatively uniform gray or brown bellies; 63% of the juveniles, but no adults, have dark bellies with very contrasting distinct light spots (Fig. 2); 33% of the juveniles and 71% of the adults have dark bellies with moderate to low contrast distinct light spots or vermiculations.

Ronald I. Crombie (pers. comm.) took the following notes on a 79.4 mm SVL juvenile female (USNM 302192): "Light markings on back rich tan, especially on head, darker markings deep wood brown. Warts on side with reddish brown markings. Venter gray with lighter gray spots, lighter marks distinctly greenish in groin and under legs. Red-brown pustules under arms and near axilla (parasites?). Rear of thighs black with a few greenish blotches and some red-brown ones near anus. Soles of hands and feet dark gray, feet almost black. Iris gold with brassy vermiculations above, dark below." Crombie noted that on two other large juveniles (USNM 302194, 72.3 mm SVL; USNM 302195, 69.8 mm): "Considerable red spotting on anterior and posterior thighs." Charles W. Myers (pers. comm.) took color notes for adults and juveniles: "Adults [AMNH 128021–128022 = CWM 18514, 18516]: Throats blackish gray; rest of ventral surfaces gray, with or without small white spots. Thighs above with black bands separated by brown interspaces that may have a faint reddish suffusion (not bright as in juveniles). Rear of thigh black with a line of silvery white dots. Iris pale bronze with reddish brown horizontal stripe. Juveniles [AMNH 128023–128031 = CWM 18526–18534]: Throat and other ventral surfaces gray with irregular white spotting. Thighs with black bands and bright orange-red interspaces antero- and posterodorsally (red color not continuous across dorsal midline of thigh). Iris pale bronzy gray on upper half—above an ill-defined reddish brown horizontal stripe—and with a faint reddish suffusion on lower part of iris."

The degree of juvenile and adult pattern

differences from the same locality is striking in preserved specimens. The most noticeable differences occur on the thighs. The upper portion of the posterior thigh surfaces in juveniles have well defined large light spots (bright red in life), whereas such spots are not distinct or completely absent in adults. In most juveniles, there is a distinct light longitudinal band on the mid-ventral thigh surfaces; no such distinct light band occurs in adults. The belly spotting differences between juveniles and adults are not as striking as the thigh surface pattern differences—in juveniles, the dark bellies have more distinct light spots than adults.

No dorsolateral folds are evident in 16% of the individuals examined. In most specimens (77%) dorsolateral folds are distinct, but broken (not continuous) and range from short (extending only to the shoulder region) to long (entire length of back from behind eye to leg). Only two individuals have almost continuous dorsolateral folds extending to the sacrum, and only one specimen has a continuous dorsolateral fold extending to the leg.

Most specimens have a shagreen and white tubercles on the dorsum. When tubercles are present, they are more abundant on the posterior dorsum. Only in juveniles (60%) is a strong warty shagreen developed.

The upper shank usually has a shagreen (93%). Most specimens (87%) have few to many black and/or white tubercles; some (13%) have very few or no tubercles.

The texture of the outer tarsus is usually shagreened (85%). Most specimens (93%) have few to many black and/or white tubercles; a few (7%) have very few or no tubercles.

The texture of the sole of the foot is usually smooth (87%); 11% have a weak shagreen; only one individual has scattered white tubercles.

Adult males have one black spine on each thumb. There is no indication of chest spines, chest tubercles, or chin tubercles.

Vocal sacs are neither laterally expanded nor differentially patterned.

Adult females range from 103.8 to 112.9 mm SVL, adult males 74.2 to 116.8 mm SVL. The relatively small sample size does not justify analyzing the measurement data with principal components to identify potential outlier individuals.

No tadpoles are available for this group.

Habitat notes are available from two sets of collectors from the same rock outcrop from Mucajaí, Roraima, Brazil. Charles W. Myers (pers. comm.) indicated for specimens AMNH 128021–128031, collected on 11 July 1987: “On granite inselberg surrounded by humid scrubby forest with many palms. Some juveniles by day under granite flakes microsympatric with *Tropidurus hispidus* and *Leptodactylus fuscus*. Other juveniles by night, sitting on bare rock or in small pools of water (with sparse aquatic vegetation) on the bare rock. The four adults all in the small pools by night.” On 30 May–1 June 1988, Ronald I. Crombie (pers. comm.) collected USNM 302066–302068, 302190–302203, MZUSP 660889 at night from on or under rock. Ronald I. Crombie (pers. comm.) documented that USNM 302267 from Colônia Apiaú, Roraima, Brazil, collected on the afternoon of 14 June 1988, was taken from under roofing tiles at an abandoned hunting camp in the forest, not near any rocky outcrop.

Group 4.—Specimens in this group are from French Guiana and Surinam (Fig. 1). One adult female, 1 adult male (both from French Guiana), 54 total specimens.

Most specimens have two large, dark, relatively well-defined blotches on the dorsum posterior to the dark interorbital blotch (Heyer 1979, fig. 1, pattern K); these blotches may be outlined by a white ring or a dark border. A few specimens have some paired large or small dark spots on the dorsum (Heyer 1979, fig. 1, patterns H, J). A few have fused blotches (Heyer 1979, fig. 1, patterns D, I). Uniform patterns (Heyer

1979, fig. 1, pattern C) occur in 9% of the sample.

Upper lips demonstrate variability among the following states. Seven percent of the specimens have little pattern on the upper lip (Heyer 1979, fig. 2, patterns C, E); 54% have some expression of alternating light and dark vertical bars (Heyer 1979, fig. 2, patterns A, J); 13% have some form of alternating light and dark oblique bars (Heyer 1979, fig. 2, pattern N); and 26% have some sort of irregularly defined light area in the loreal region which may extend to under the eye (Heyer 1979, fig. 2, patterns K, M).

The posterior thigh surface patterns are quite variable. They are distinctly mottled with small irregular light marks in 13% of the individuals (Heyer 1979, fig. 3, patterns C, D); distinctly mottled with large light irregular spots and marks in 13% (Heyer 1979, fig. 3, patterns A, F, K); mottled with some expression of light vertical marks or bars on the upper portions of the thigh surfaces in 11% (Heyer 1979, fig. 3, pattern I); mottled with large distinct light spots or blotches on the upper portions of the thigh surfaces (light marks may be confluent with each other) in 51% of the individuals; one individual has distinct light spots on the posterior thigh surfaces (Heyer 1979, fig. 3, pattern N); three specimens have some large dark blotches on the lower portion of the thigh surfaces; two specimens have relatively uniform thigh surfaces.

Juveniles do not have a distinct light band lengthwise in the middle of the ventral thigh surfaces, although 21% of the juveniles have a noticeable light band (Fig. 2), neither adult has any indication of a light band; 21% of the juveniles have very light ventral thigh surfaces with few or no melanophores, neither adult has this pattern; no juveniles have almost uniformly dark ventral thigh surfaces, one adult has this pattern; 4% of the juveniles have lightly to moderately mottled ventral thigh surfaces, one adult has heavily mottled ventral thigh surfaces; 50% of the juveniles have the up-

per-lateral sector of the ventral thigh surfaces boldly mottled with the rest of the ventral thigh surface uniformly light, neither adult has this pattern.

No juveniles, but both adults, have a relatively uniform gray/brown belly; 23% of the juveniles have a uniform and light belly with very few melanophores; 27% of the juveniles have a dark belly with distinct light spots/vermiculations of moderate to low contrast; 25% of the juveniles have a mottled belly of smaller irregular light areas on a darker ground; 25% of the juveniles have a bold mottled belly pattern of large light spots/flecks on a darker ground (Fig. 2).

Dr. Charles W. Myers (pers. comm.) took color notes on a series of juvenile specimens from Voltzberg, Surinam (AMNH 87705–87736): “Dorsal surfaces brown with a remarkably constant pattern of darker brown markings that are outlined in light yellowish brown. Top of thigh with orange-red flash mark (which is concealed in frog’s normal position) that is broken by black bars; the flash mark is present in all but is quite faint on several specimens of different size. Rear of thigh black with pale blue or greenish blue dots. Venters white with variable amounts of gray mottling, turning light gray underneath limbs. Iris pale bronzy orange, in some individuals turning pale gray below pupil; dense black venation and a tendency for a brownish horizontal streak.”

There is no locality for which a series of adults and juveniles are available. In comparing adults and juveniles from different localities, the degree of adult and juvenile pattern differences in preserved specimens is noticeable but not striking. Most noticeable are the upper posterior thigh light spots/blotches (red in life) on juveniles, that are not present in either adult. The bellies and ventral thigh surfaces are much lighter than in the adults, with the smallest juveniles having the lightest bellies, with a size gradient of darkening evident.

Almost all individuals (94%) have some

sort of dorsolateral fold development (the 4 individuals scored as having no indication of dorsolateral folds perhaps due to preservation artifact?); 34% of the specimens have a pair of entire dorsolateral folds extending from behind the eye to at least as far as the sacrum; 60% of the individuals have a pair of interrupted folds to a series of ridges or elongate warts to at least the sacral region.

All individuals have at least a weakly-developed dorsal shagreen. Two juveniles have a pronounced shagreen with small bumpy glands. Thirty-one percent of the juveniles have at least a few tubercles on the dorsum, that are more abundant posteriorly. Both adults have a weakly developed dorsal shagreen; one lacks noticeable tubercles, the other has very few white dorsal tubercles.

Most specimens have a shagreen on the dorsal shank surface (lacking in only two). Most specimens (89%) have few to many white tubercles; few specimens (11%) have very few or no white tubercles.

The texture of the outer tarsus may be shagreened or not. Many specimens (70%) have few to many white tubercles; some specimens (30%) have very few to no white tubercles.

Only two specimens have a weak shagreen on the sole of the foot; only one specimen has a few white tubercles; all others have a smooth sole that is lacking shagreen or tubercles.

The single adult male has one white spine on each thumb and one white bump on each prepollex. There is no indication of chest spines, chest tubercles, or a patch of tubercles on the chin. Vocal sacs are neither laterally expanded nor differentially pigmented.

The adult female is 111.2 mm SVL, the adult male 117.6 mm SVL.

No tadpoles are available for this group.

Habitat data are available from Saramacca, Surinam (Charles W. Myers, pers. comm.) for AMNH 87705–87736 collected 23 February 1972 from a granite outcrop:

“Three specimens of a considerably larger *Leptodactylus* [not collected] were seen on the granite at night, but when approached they backed under rock crevices in which lizards were sleeping. [Following notes for juveniles.] Several by day, under rock flakes around edges of bare granite surfaces; a few in pools in circular depressions after afternoon rain, an hour or so before dark. Most however at night, when they proved to be exceedingly abundant out on bare rock far away from any cover or crevice. The majority were sitting in the little damp gullies that resulted from overflowing of water from the circular holes and other depressions on the granite.”

Intergroup differentiation and evaluation of species limits.—The group characterizations described in the preceding section are used to evaluate differentiation among the groups. In addition, some data are available for two or three of the groups that pertain to group differentiation. These additional data are presented below.

The preceding group characterizations demonstrate that the greatest differentiation occurs between the combined Groups 1 and 2 on the one hand and Groups 3 and 4 on the other. The most distinctive differentiating characteristics are size of adults, secondary male features, and contrast of juvenile and adult color patterns (Table 1).

Discriminant function analyses using measurement data support this clustering, although there are not enough data to include Group 4 in the analyses. Data run separately for males and females show the same results. Results of the male data show somewhat less differentiation among groups, so they are described as examples for both sets of analyses. Data for the Group 4 individual were not used in estimating the multivariate models. The posterior classifications based on group discriminant function means for Groups 1, 2, and 3 result in rather good group assignments overall, but most robust for Group 3, with only one male being posteriorly assigned to the wrong group (Group 1, Table

Table 1.—Distribution of certain characteristics among four groups of rocky habitat *Leptodactylus* from northern South America. Group 1 is from Colombia and nearby Venezuela, 2 from southeast Venezuela and Guyana, 3 from northern Brazil, 4 from Surinam and French Guiana.

	Group 1	Group 2	Group 3	Group 4
Female size in mm	55–78	54–74	104–113	111
Male size in mm	45–71	51–72	74–117	118
Number of spines/thumb in males	1	1–2	1	1
Chest spines in males	+	+	–	–
Band of chest tubercles in males	+	–	–	–
Chin tubercles in males	+	–	–	–
Vocal sacs laterally expanded and darkly pigmented	+	+	–	–
Juvenile and adult color patterns strikingly different	–	+	+	–

2). The graphical results when the first canonical factor is plotted against the second (Fig. 3) indicates that Group 3 individuals are separated from Group 1 and 2 individuals along the first axis, typically size related, which is consistent with the adult size distributions of the three groups. The single Group 3 individual that was posteriorly classified as belonging to Group 1 rather than 3 (USNM 302202) is the left-most symbol for Group 3 individuals in Fig. 3 and is the smallest male in the Group 3 sample.

Some micro-complement fixation tests, comparing albumins of some of these frogs included one sample from Group 2 and one sample from Group 3. Although materials were insufficient to raise antisera to either the Group 2 or Group 3 specimens, both samples were tested against antisera to albumins of other members of the *L. pentadactylus* species group. Results (Table 3) indicate that the Group 2 and Group 3 sam-

Table 2.—Discriminant function analyses for male data for Groups 1 (Colombia and nearby Venezuela), 2 (southeast Venezuela and Guyana), and 3 (northern Brazil).

	Number of observations classified into groups		
	Group 1	Group 2	Group 3
Group 1	26	5	0
Group 2	4	31	0
Group 3	1	0	12

ples are not identical and, in fact, suggest that they are quite different.

Thus, the data are unequivocal that at the very least, Groups 1 and 2 combined represent a distinct species from Groups 3 and 4 combined. The more difficult questions to resolve are whether Group 1 represents a species distinct from Group 2 and whether Group 3 represents a species distinct from Group 4. Each of these two situations is discussed in turn.

The greatest differences between Group 1 and Group 2 individuals are with male secondary sexual characteristics (Table 1). Whereas males in Group 1 have chin tubercles and, in the larger adults, a band of chest tubercles, no males in Group 2 have such tubercles. Whereas some males in Group 2 have two spines per thumb, all males in Group 1 have but one spine per thumb. There are differences in terms of degree of expression of states in the upper lip patterns, posterior thigh surface patterns, ventral thigh surface patterns, belly patterns, outer tarsal texture, and foot texture. Whereas there is complete overlap of adult sizes between the two groups, there is some morphological differentiation demonstrated by measurement data (Fig. 3). There is clearly some separation of Group 1 from Group 2 along the second canonical factor, indicating some differentiation of shape. The dependent variables that have the highest values on the second canonical factor

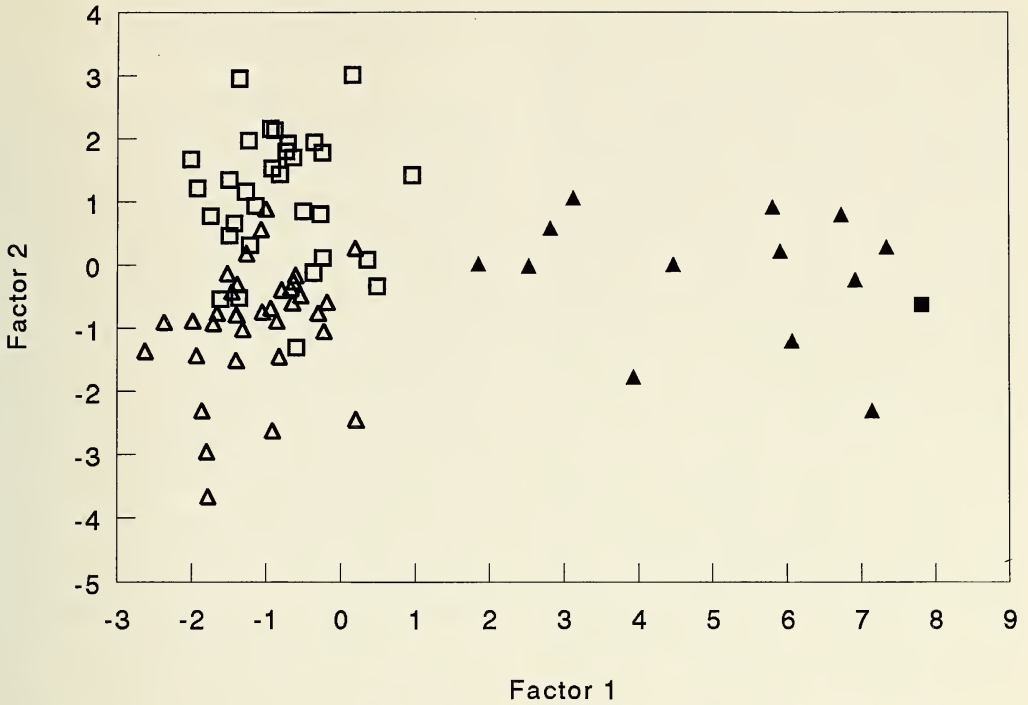


Fig. 3. Graph of first and second canonical factors for Group I-IV males. Group I = open squares, Group II = open triangles, Group III = filled triangles, Group IV = filled square.

for females are shank length (0.275), head length (0.253), thigh length (0.251), eye-nostril distance (0.250), and head width (0.236) and for males are thigh length (-0.512), shank length (-0.493), eye-nostril distance (-0.446), and foot length (-0.413), suggesting an overall shape difference. Given the discrete differences of male secondary sexual characteristics, combined with the evidence of demonstrable

differentiation in pattern and morphology between Groups 1 and 2, the evidence is most consistent with recognizing members of these two groups as distinct species.

Evaluating the differentiation between Groups 3 and 4 is confounded by the fact that there is but a single adult male and a single adult female available for Group 4. In comparing the available data, there is less apparent differentiation between Groups 3 and 4 than between Groups 1 and 2 (also see Table 1). Group 3 juveniles differ from Group 4 juveniles in terms of ventral coloration pattern. Group 3 juveniles often have a very distinct longitudinal light band on dark ventral thigh surfaces; no Group 4 juveniles have this expression. Group 3 juveniles often have very light patterns over the entire ventral thigh surface; no Group 4 juveniles have this expression. Most Group 3 juveniles have very contrasting belly patterns of distinct light spots on

Table 3.—Immunological distances between albumins of two samples of northern South American granitic outcrop associated *Leptodactylus*.

Samples	Immunological distance			
	Anti-serum- <i>L. pentadactylus</i>	Anti-serum- <i>L. fallax</i>	Anti-serum- <i>L. flavopictus</i>	Anti-serum- <i>L. labyrinthicus</i>
Group 2 (Bolívar, Venezuela)	67	24	43	57
Group 3 (Roraima, Brazil)	22	30	57	43

a dark belly; no Group 4 juveniles have this pattern. As a consequence of these differences in juveniles, the contrast between juvenile and adult ventral patterns is more pronounced in Group 3 than in Group 4. The single adult male in Group 4 is 117.6 mm SVL, minimally larger than the largest Group 3 male, 116.8 mm SVL. The Group 4 male has a single white spine on each thumb and the merest indication of a second spine. White thumb spines in *Leptodactylus* occur due to two different reasons. They are characteristic of very young males, which have just become sexually mature, and some *Leptodactylus* seasonally shed the black keratin sheath of the spine. If the white spine condition of the Group 4 male is because it is a young male, then there is probably a size difference between Group 3 and 4 adults. When actually comparing the available adults from Group 3 and 4 side-by-side, I find no differences among them other than the male thumb condition noted. The data indicate that there has been some differentiation between Groups 3 and 4, but the data are not at all conclusive in deciding whether Groups 3 and 4 represent one or two species. Given the lack of advertisement calls and adequate samples of adults of Group 4, I prefer to take the nomenclaturally conservative (and very possibly the biologically incorrect) position of recognizing a single species for Group 3 and Group 4 combined.

Nomenclature.—Only a single name has been proposed for any of the frogs involved in this portion of the study: *Leptodactylus rugosus* Noble, 1923. As Donnelly & Myers (1991:23) pointed out, the holotype (AMNH 1169, 38 mm SVL) from near Kaieteur Falls, Guyana, described as an adult by Noble (1923:297), is in fact a juvenile. *Leptodactylus rugosus* applies to the frogs of Group 2 in this paper. Without available names for the other two species recognized as distinct, they are described as the following new species.

Leptodactylus lithonaetes, new species
Figs. 4A, 5

Holotype.—AMNH 100656, an adult male from Venezuela; Amazonas, SW sector Cerro Yapacana, 600 m, 3°57'N, 67°00'W. Collected by Charles W. Myers and John Daly on 18–19 February 1978.

Paratopotypes.—AMNH 100657–100666, 100668, same data as holotype except collected from 18–22 February 1978.

Diagnosis.—The species of *Leptodactylus* that share conditions of free toes (no lateral fringe) and indistinct dorsolateral folds (at least in some individuals) with *L. lithonaetes* are *bufonius*, *labialis*, *labyrinthicus*, *laticeps*, *latinus*, *myersi*, *rugosus*, *syphax*, and *troglydites*. The upper shank and posterior tarsus of *bufonius*, *labialis*, *latinus*, and *troglydites* are covered with large prominent white tubercles and males lack thumb spines; the upper shank and posterior tarsus of *lithonaetes* has black-tipped tubercles (in some preserved specimens the black tips may be lost, leaving white tubercles which are noticeably smaller than those of *bufonius*, etc.), and the males have a spine on each thumb. *Leptodactylus laticeps* has a tile-like dorsal pattern (Heyer 1979, fig. 1, pattern F) and is larger (minimum adult SVL 91 mm) than *lithonaetes* (maximum adult SVL 78 mm), which does not have a distinct tile-like pattern. *Leptodactylus labyrinthicus* is larger (minimum adult SVL 117 mm) than *lithonaetes*; no *L. labyrinthicus* have light loreal blotches, whereas several *lithonaetes* do. *Leptodactylus myersi* is larger (females 104–113 mm SVL, males 74–118 mm SVL) than *lithonaetes* and *myersi* males lack the chest spines found on *lithonaetes*. *Leptodactylus lithonaetes* is most likely to be confused with *L. rugosus* and *syphax*; the most distinctive characteristics among these three species are male secondary sexual characteristics. *Leptodactylus lithonaetes* has a single black spine on each thumb and a patch of brown/black tubercles on the chin/throat; all *L. syphax* and some *rugosus*

have two spines per thumb and no *syphax* or *rugosus* males have a patch of chin tubercles.

Description of holotype.—Snout rounded from above and in profile; canthus rostralis indistinct; loreal weakly obtuse-concave; tympanum distinct, greatest diameter about $\frac{3}{4}$ eye diameter; vomerine teeth in strongly arched series, between and posterior to choanae, separated medially by about $\frac{1}{6}$ length of single vomerine tooth series; vocal slits present; vocal sacs expanded laterally and darkened; finger lengths in increasing order II just < IV < I just < III; extensive finger ridging best developed on medial surfaces of fingers II and III; metacarpal tubercles large, about same size, inner triangular shaped, outer ovate and bifid; arms strongly hypertrophied; thumb with one large black medial spine, one pair of large bicuspid black chest spines, narrow band of brown-black tubercles across chest, field of brown-black tubercles on thumb on either side of spine, well developed field of brown-black tubercles on chin medially extending posteriorly to about mid-throat; dorsum relatively smooth, a few scattered black tubercles posteriorly; one short pair of interrupted dark-outlined ridges behind eye and above and posterior to tympanum, well developed supratympanic fold from eye to humerus; commissural gland well developed, flanks with three large irregular glands on each side, lower posterior thigh with elongate longitudinal gland; ventral texture smooth; belly disk fold well developed; toe tips bulbous, broader than toes immediately behind tips; toes free, lacking fringe or web; subarticular tubercles well developed, ovoid; outer rounded metatarsal tubercle relatively well developed, about $\frac{1}{4}$ size ovoid inner metatarsal tubercle; tarsal fold moderately developed, sinuous, extending about $\frac{2}{5}$ length of tarsus; no metatarsal fold; outer tarsus with several brown-black tubercles; sole of foot smooth.

SVL 71.4 mm, head length 27.2 mm, head width 27.4 mm, eye–nostril distance 6.4 mm, interorbital distance 5.1 mm, great-

est tympanum diameter (including annulus) 6.3 mm, thigh length 31.5 mm, shank length 31.5 mm, foot length 36.1 mm.

Dorsum with a light interocular bar; rest of back with ill-defined pattern of series of fused blotches on each side of midline and series of darker brown flecks more numerous posteriorly; upper limbs with faint suggestion of transverse bands, most distinct on dorsal surfaces of tarsus and foot; irregular dark canthal stripe, with an irregular light tan loreal blotch ventrally; upper lip with irregular dark border. Throat almost uniformly dark brown medially, laterally expanded vocal sacs dark brown, edges of jaws with black borders; chest, belly, and ventral limb surfaces with extensive, fine brown mottling. Posterior surface of thigh with large irregular-shaped dark and light blotches.

Etymology.—From the Greek *lithos*, stone, rock and *naetes*, inhabitant, in reference to its habitat.

Variation.—Variation is described earlier in the paper under Group 1 individuals.

Larval characteristics (based on sample from Cerro Patavá, Colombia, UTA 23499, 23507–23510, $n = 10$).—Dorsal head and body relatively uniform brown, dorsal pattern ending somewhat abruptly on side of head-body; oral disk lacking melanophores; belly with or without white flecks; ventral region anterior to guts with melanophores visible under skin; tail dorsal fin and most of muscular region mottled, with or without darker flecks and/or weakly-developed light ocelli; ventral musculature and tail fin lacking melanophores entirely or with melanophores on distal half, most heavy at tip region; nostril nearer eye than tip of snout; internarial distance greater than interorbital distance; eye diameter 14–16% head-body length; oral disk width 25–26% head-body length for Gosner stages 28–29, 22–26% head-body length for Gosner stages 35–40; anterior oral papilla gap 80–88% oral disk width; 32–34 denticles on one side of split tooth row anterior to beak (row A-2) for Gosner stages 28–29, 42–51 denticles for

a**b**

Fig. 4. New species of *Leptodactylus*. A. Male paratopotype (AMNH 100668) of *Leptodactylus lithonaetes*. Photograph courtesy of C. W. Myers, American Museum of Natural History. B. Male paratopotype (AMNH 128021) of *Leptodactylus myersi*. Photograph courtesy of C. W. Myers, American Museum of Natural History.

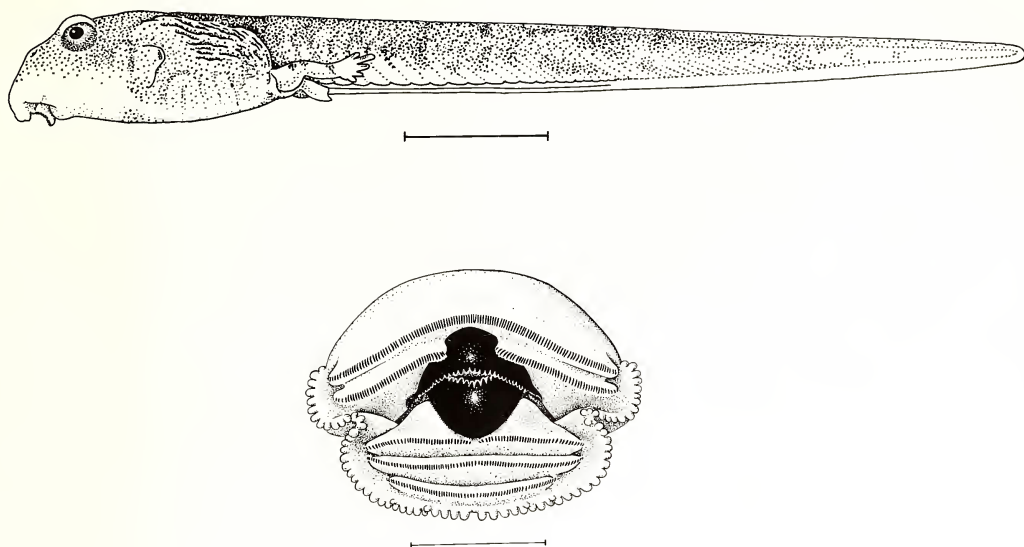


Fig. 5. Lateral view and mouthparts of larval *Leptodactylus lithonaetes*. Scale bars 5 and 1 mm respectively. Diagrammatic illustrations based on specimen from UTA-A 23509, Gosner stage 38.

Gosner stages 35–40; upper beak width 11–12% head–body length; upper beak depth 30–33% upper beak width for Gosner stages 28–29, 27–37% for Gosner stages 35–40; single row of marginal papillae; tooth row formulae 2(2)/3 or 2(2)/3(1); field of glandular ridges on body above abdominal cavity; spiracle sinistral; vent median; fins 29–33% tail depth at maximum tail depth for Gosner stages 28–29, 23–36% for Gosner stages 35–40; body depth 38–42% head–body length for Gosner stages 28–29, 42–48% for Gosner stages 35–40; body width 55–56% head–body length for Gosner stages 28–29, 58–64% for Gosner stages 35–40; body depth 70–75% body width for Gosner stages 28–29, 67–74% for Gosner stages 35–40; head–body length 32–35% total length for Gosner stages 28–29, 28–31% for Gosner stages 35–40; total length, stage 38, 36.1 mm (Fig. 5).

Advertisement Call.—Not recorded.

Karyotype.—Unknown.

Referred specimens (specifically not designated as types).—COLOMBIA. AMAZONAS: Río Igará-Paraná, 50 km arriba “La Chorrera,” IND-AN 2822. GUAINÍA:

Puerto Inírida, Río Atabapo, IND-AN 2808, 2811; Río Negro, opposite Casiquare Canal and Guainía, AMNH 23160–23162. VAUPES: Cerro Patavá, IND-AN 3399, UTA-A 3724–3725, 3772–3785, 3857–3877, 23499–23500 (larvae), 23503–23510 (larvae). VICHADA: Parque Nacional Natural El Tuparro, ICNMNH 14045–14047, IND-AN 2303–2304, 3736; Puerto Carreño, Cueva de Arévalo, ICNMNH 13970–13996.

VENEZUELA. AMAZONAS: Canaripo, RMNH 23913–23916, 23931–23950, 23970–23973 (plus 5 unnumbered juveniles and metamorphs and 3 larvae); Cerro Yapacana, AMNH 100667 (skinned specimen); Mision Coromoto-Atures, USNM 137186–137192; Puerto Ayacucho, AMNH 23209–23219, FMNH 175460–175465, 176197–176201, 176203–176222, KU 207531–207533, USNM 80634, 80665–80673, 291081–291082; Sanariapo, MCZ 27827, USNM 80635–80639. APURE: Hato Caribén, 46 km NE Puerto Páez, Río Cinaruco, USNM 216795–216797. BOLÍVAR: 3 km E Río Orinoco just below Río Horeda, 100 m, AMNH 62169; mouth of Río Parguaza, AMNH 62168.

Leptodactylus myersi, new species

Fig. 4B

Holotype.—MZUSP 66089, an adult male from Brazil; Roraima; Mucajá, 2°25'N, 60°55'W. Collected by Celso Morato de Carvalho and Ronald I. Crombie on 31 May 1988.

Paratopotypes.—AMNH 128021–128031, MZUSP 70976–70986 collected by Celso Morato de Carvalho, Charles W. Myers, Thelma Schmidt, and P. E. Vanzolini on 11 July 1987, USNM 302190–302203, collected by Celso Morato de Carvalho and Ronald I. Crombie on 30 May–1 June 1988, USNM 302204–302205, collected by Carvalho and Crombie on 20 June 1988.

Diagnosis.—The species of *Leptodactylus* that share conditions of free toes (no lateral fringe) and indistinct dorsolateral folds (at least in some individuals) with *L. myersi* are *bufonius*, *labialis*, *labyrinthicus*, *laticeps*, *latinasus*, *lithonaetes*, *rugosus*, *syphax*, and *troglydites*. The upper shank and posterior tarsus of *bufonius*, *labialis*, *latinasus*, and *troglydites* are covered with large prominent white tubercles and males lack thumb spines; the upper shank and posterior tarsus of *myersi* has black-tipped tubercles (in some preserved specimens the black tips may be lost, leaving white tubercles which are noticeably smaller than those of *bufonius*, etc.) and the males have a spine on each thumb. *Leptodactylus laticeps* has a very distinct tile-like dorsal pattern (Heyer 1979, fig. 1, pattern F); *L. myersi* does not have a tile-like dorsal pattern. *Leptodactylus labyrinthicus* is larger (minimum adult SVL 117 mm) than *myersi*; all large (>170 mm SVL) male *labyrinthicus* have chest spines, no *myersi* males have chest spines. *Leptodactylus syphax* is smaller (maximum adult SVL 78 mm) than *myersi* (maximum adult SVL 118 mm) and male *syphax* have two spines per thumb in contrast to the single thumb spine found in *myersi*. *Leptodactylus lithonaetes* and *rugosus* are smaller (maximum adult SVL 78 mm) than *myersi*. The males of *L. lithon-*

aetes and *rugosus* have laterally expanded vocal sacs; the male vocal sacs of *L. myersi* are not expanded externally.

Description of holotype.—Snout nearly rounded from above and rounded in profile; canthus rostralis indistinct; loreal obtuse-concave; tympanum distinct, greatest diameter about $\frac{2}{3}$ eye diameter; vomerine teeth in arched series, between and posterior to choanae, separated medially by about $\frac{1}{4}$ length of single vomerine tooth series; vocal slits present; vocal sac single, internal; finger lengths in increasing order II just < IV < I just < III; finger ridges well developed medially on fingers II and III; inner and outer metacarpal tubercles large, about same size, outer bifid; arms moderately hypertrophied; thumb with one large black medial spine; no chest spines; band of black tubercles across chest, on ventral surfaces of upper arms, on flanks near axilla and along lateral edges of jaws ventrally; dorsum relatively smooth, a few small black or white tubercles scattered posteriorly; extensively interrupted pair of dark-outlined dorsolateral folds from eye to beyond sacrum, distinct continuous supratympanic fold from eye to humerus; flanks glandular; belly smooth; belly disk fold discernible but weak; toe tips bulbous, broader than toe widths just behind tips; toes ridged laterally, especially on toes I, II, and III, not developed into fringe; subarticular tubercles well developed, ovoid; outer metatarsal tubercle round, flattened, about $\frac{1}{2}$ size of ovoid inner tubercle; tarsal fold well developed, extending about $\frac{2}{3}$ length of tarsus; no metatarsal fold; outer tarsus with a few small white or black tubercles; sole of foot smooth.

SVL 109.4 mm, head length 47.2 mm, head width 44.1 mm, eye–nostril distance 9.9 mm, interorbital distance 8.4 mm, greatest tympanum diameter (including annulus) 7.8 mm, thigh length 47.2 mm, shank length 44.1 mm, foot length 46.8 mm.

Dorsum dark gray brown with irregular darker brown interorbital blotch and two darker dorsal chevrons, one in shoulder re-

gion, one in sacral region; dark well-defined canthal stripe; upper lip rather uniform gray-brown; upper limbs transversely banded. Venter dark and gray, chin and throat uniform, chest and belly with indistinct light, small vermiculations. Upper portion of posterior thigh surface with extension of dorsal band pattern, lower portion with black elongate oval region containing a few contrasting small light regular and irregular spots.

Etymology.—Named for Dr. Charles W. Myers for his contributions to Neotropical herpetology in general and bringing this new species to my attention in particular.

Variation.—Variation is described earlier in this paper under Group 3 and Group 4 individuals.

Advertisement Call.—Unknown.

Karyotype.—Unknown.

Referred Specimens (specifically not designated as types).—BRAZIL.¹ AMAZONAS: Rio Aracá (Serrinha), MZUSP 59016, 59018, 59026-59028. RORAIMA: Colonia Apiaú, MZUSP 65949, USNM 302267; Mucajaí, USNM 302206 (guttured and partially deboned).

FRENCH GUIANA. No further locality, MNHN 1982-81; Massif des Emerillons, MNHN 1982-82; Montagne St. Marcel, MNHN 1982-73-1982-80; Montagne des Trois Pitons, MNHN 1982-153; Peolaëu (Haut Oyapock), MNHN 1982-83; Trois Saut, MNHN 1982-84.

SURINAM. BROKOPONDO/NICKERIE: Tafel Berg, 1025 m, MCZ 97259-97261, 97299, 97303, 97306, 97308, RMNH 23912, 23919-23930, 23951-23961. NICKERIE: Amotopo, RMNH 23964-23968; Blanche Marie-Vall, RMNH 23910-23911. SARAMACCA: Raleighval-

len-Voltzberg Nature Preserve, MCZ 92363; Voltzberg, RMNH 23974-23976.

Disposition of Specimen from Paraguay

On 22 July 1973, the mammalogist Philip Myers collected a single specimen of *Leptodactylus*, MVZ 111027, that resembles *L. syphax* from a rocky region with caves 1 km S of Tobatí, La Cordillera, Paraguay (25°15'S, 57°04'W). The same cave system has been re-collected by mammalogists, who have also collected whatever frogs they encountered (P. Myers, pers. comm.). Even though these newer collections contain *Leptodactylus*, none of them are the same species as MVZ 111027.

Description of the adult female from near Tobatí follows: tympanum large, greatest diameter about $\frac{7}{8}$ eye diameter; vomerine teeth in arched series posterior to the choanae, contacting medially; palatine teeth present; inner metacarpal tubercle ovoid, the outer (about same size as inner) somewhat rounded, tubercles separated by less than width of inner tubercle; dorsum glandular and smooth; supratympanic fold distinct, no other folds present; no distinct glands other than the general glandular structure of skin on top of shanks and on back; venter smooth; ventral disk not well defined; tips of toes barely swollen; toes lacking fringe or web; no metatarsal fold; tarsal fold weakly developed extending about $\frac{3}{5}$ length of tarsus; dorsal shank and outer tarsus surfaces glandular with scattered white tubercles; sole of foot smooth; side of head uniform brown; dorsum brown with faint quadrangular ocellations; upper arm surfaces almost uniform brown; upper leg surfaces weakly cross banded with darker brown; venter cream, lacking melanophores; posterior surfaces of thighs distinctly mottled, almost spotted; SVL 79.7 mm, head length 31.7 mm, head width 29.1 mm, eye-nostril distance 7.4 mm, tympanum diameter 6.5 mm, thigh length 28.7 mm, shank length 30.0 mm, foot length 30.6 mm.

¹ After the manuscript was submitted for publication, another locality for *L. myersi* was discovered in the collections at MZUSP. MZUSP 28405, 54110-54114 are from Brazil, Pará, Igarape Jaramacaru, Campos do Ariramba, 1°09'S, 55°54'W. The frogs were collected from sandstone formations (P. E. Vanzolini, pers. comm.), a common feature within the Campos do Ariramba region (Egler 1960).



Fig. 6. Known distribution of *Leptodactylus syphax* in Brazil and Paraguay. Political boundaries outlined for Brazil and Paraguay. Map truncated at 40°S.

The Tobatí specimen is very similar to *L. syphax* from Brazil. They are the same size and share the same features of pattern and texture. The shared pattern of a low-contrast mosaic pattern of quadrangular ocellations is uncommon in the genus. The striking visual difference between the Tobatí specimen and Brazilian *L. syphax* is the short leg of the Tobatí specimen. The thigh/SVL, shank/SVL, and foot/SVL ratios for the Tobatí specimen are 36%, 38%, and 38% respectively. The mean female ratios for *L. syphax* are 42%, 42%, and 44% respectively. The only other feature that differs between the Tobatí specimen and Brazilian *L. syphax* is that the subarticular tubercle on the thumb of the Tobatí specimen is less pronounced than in Brazilian *L. syphax*.

Without additional material, it is impossible to know whether the short leg of MVZ 111027 is characteristic of the population or is an individual aberration. The species identification of the Tobatí deme is made more difficult by the lack of both advertisement call data and information on male secondary sexual characteristics. Given the available data, I think the best taxonomic

conclusion is to consider that the Tobatí specimen is conspecific with *L. syphax*. This conclusion should only be taken as a working hypothesis until further data become available. The geographic extension into Paraguay of *L. syphax*, although considerable, might be expected given the disjunct nature of the rest of the known populations of *L. syphax* (Fig. 6).

Discussion

The main conclusion of this study is that there is considerably more variation among populations of *Leptodactylus* associated with rocky habitats than previously summarized (Heyer 1979). Fully understanding and interpreting that variation is not possible at this time. Two suites of questions are raised: those associated with distributions and those associated with relationships.

The degree of habitat restriction to rocky habitats, either streambeds or outcrops, is not known for certain, but such habitat fidelity is high, if not complete. The semi-terrestrial larval ecomorph of *L. lithonates* and *rugosus* is certainly an adaptation associated with rocky substrates and probably

flowing water. The larvae of *L. myersi* and *syphax* are unknown, but adults and juveniles of both have been collected most frequently (entirely so for *L. syphax*) from rocky outcrops. The scanty data suggest a greater association of *L. lithonaetes* and *rugosus* with rocky streams (either in a granite or sandstone setting) and *L. myersi* and *syphax* with granitic or sandstone outcrops. The patchy distributions of the taxa also indicate a high fidelity to rocky habitats, which themselves are patchily distributed. This habitat fidelity allows prediction of where the species should occur in areas where they have not been collected up to the present. For example, the easternmost locality in Colombia for *L. lithonaetes* (Amazonas, Río Igará-Paraná), coincides reasonably well with an isolated occurrence of Precambrian-aged rocks with granite being among the most common rock types (Kroonenberg 1985, fig. 1, p. 58). There are additional isolated patches of Precambrian rocks of the same formation in Colombia (Kroonenberg 1985:58) from which *L. lithonaetes* are currently unknown. *Leptodactylus lithonaetes* would be expected to occur (at least historically, if not currently) on these Precambrian rock formations if running water exists in the formations.

There are several questions remaining regarding relationships. Although *L. lithonaetes* is considered distinct from *rugosus* in this paper, it is possible that the differences between the two taxa represent (pronounced) geographic differentiation in a single species. On the other hand, the differences herein interpreted to represent geographic variation between the Surinam and French Guiana populations of *L. myersi* and the Roraima, Brazil, populations of *myersi*, may be too conservative an interpretation and two species should be recognized instead. The species allocation of the frogs from Brazil, Amazonas, Rio Aracá need verification. At present, only rather small-sized juveniles are available from the Rio Aracá site. The characteristics they have are consistent with being conspecific with *L.*

myersi (my best guess), or *L. lithonaetes*, or representing yet another new species. The Paraguayan population needs resampling to verify whether it is conspecific with *L. syphax*. It is very likely that advertisement call data could resolve the outstanding species level problems. At another level, the available data can not answer the question whether the rocky habitat associated species of *Leptodactylus* are a monophyletic cluster, having a common ancestor that became adapted to the habitat, or not. Larval information for *L. myersi* and *syphax* may resolve this question, but it is more likely some appropriate molecular based analysis is needed to answer it.

Given the many questions about relationships, any detailed discussion of zoogeography of these species is premature.

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